Community- and ecosystem-level effects of multiple environmental change drivers

DE LAENDER, Frederik

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Title: Community- and ecosystem-level effects of multiple environmental change drivers: beyond null model testing

Running head: From null models to theory-based predictions

Author and affiliation: Frederik De Laender, Research Unit in Environmental and Evolutionary Biology, Namur Institute of Complex Systems, and the Institute of Life, Earth, and Environment, University of Namur, Belgium. T: +32478429761; Frederik.delaender@unamur.be

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Abstract:

Understanding the joint effect of multiple drivers of environmental change is a key scientific challenge. The dominant approach today is to compare observed joint effects with predictions from various types of null models. Drivers are said to combine synergistically (antagonistically) when their observed joint effect is larger (smaller) than that predicted by the null model. Here, I argue that this approach does not promote understanding of effects on important community- and ecosystem-level variables such as biodiversity and ecosystem function. I use ecological theory to show that different mechanisms can lead to the same deviation from a null model's prediction. Inversely, I show that the same mechanism can lead to different deviations from a null model's prediction. These examples illustrate that it is not possible to make strong mechanistic inferences from null models. Next, I present an alternative framework to study such effects. This framework makes a clear distinction between two different kinds of drivers (resource ratio shifts and multiple stressors) and integrates both by incorporating stressor effects into resource uptake theory. I show that this framework can advance understanding because of three reasons. First, it forces formalisation of "multiple stressors", using factors that describe the number and kind of stressors, their selectivity and dynamic behaviour, and the initial trait diversity and tolerance among species. Second, it produces testable predictions on how these factors affect biodiversity and ecosystem function, alone and in combination with resource ratio shifts. Third, it can fail in informative ways. That is, its assumptions are clear, so that different kinds of deviations between predictions and observed effects can guide new experiments and theory improvement. I conclude that this framework will more effectively progress understanding of global change effects on communities and ecosystems than does the current practice of null model testing.

Null models to study the joint effects of multiple environmental change drivers

Ecosystems today are invariably challenged by a multitude of environmental change drivers (Brook *et al.*, 2008; Crain *et al.*, 2008; Halpern *et al.*, 2015; Halpern *et al.*, 2008; Schäfer *et al.*, 2016). Understanding their joint effect is a pressing scientific and societal need (Côté *et al.*, 2016; Dupont & Pörtner, 2013; Rudd, 2014). During past years, substantial effort has been put in quantifying such joint effects, with many studies focusing at the physiological level (Brennan & Collins, 2015; Gunderson *et al.*, 2016; Häder & Gao, 2015; Sokolova, 2013), while fewer have addressed how the effects of individual drivers scale up to affect higher levels of biological organisation such as communities and ecosystems (Garnier *et al.*, 2017).

The dominant approach to examine effects of multiple drivers is to use null models. These null models predict joint effects based on the effects elicited by the individual drivers. When the observed joint effects are smaller than or greater than those predictions, so-called 'antagonistic' or 'synergistic' effects are concluded, respectively (Crain *et al.*, 2008). A variety of null models exists, each with their own assumptions and limitations (Piggott *et al.*, 2015), and comprehensive overviews exist in the literature (Schäfer & Piggott, 2018). In general, these null models differ in their underlying assumption on how drivers combine to affect the biological variable of interest. The most frequently used null model is additive: it assumes that the effects of the individual drivers add up, correcting for non-independence among drivers if needed. The null model approach is applied to study effects at all levels of biological organisation, going from the individual to the community-level, and are used in both primary studies and meta-analyses (Crain *et al.*, 2008; Darling & Cote, 2008; Jackson *et al.*, 2016; Tolkkinen *et al.*, 2015).

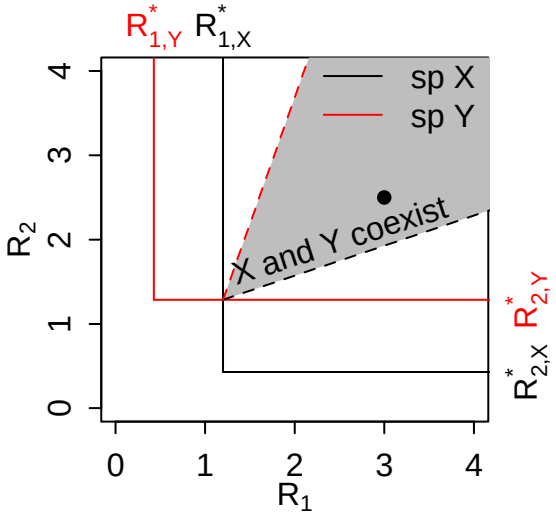
Null models do not advance comprehension of community and ecosystem-level effects.

The application of null model testing to community- and ecosystem-level effects of multiple drivers has been criticized before (Kroeker *et al.*, 2017; Thompson *et al.*, 2018). Most of these critiques revolve around the fact that drivers combine differently at different levels of biological organisation (Schäfer & Piggott, 2018). For example, additivity of effects at the level of populations does not automatically imply additivity at the community level (Kroeker *et al.*, 2017). To remediate this difficulty, the development of new null models has been recently proposed (Thompson *et al.*, 2018). In this opinion, however, I propose an alternative solution: to move away from testing null models on community and ecosystem data. My main argument to do so is that current null model testing at the level of communities and ecosystems does not advance comprehension. While null model testing has certainly facilitated meta-analyses, it has until now not augmented general insight in the mechanisms linking environmental change, multiple drivers, and biodiversity and ecosystem function (De Laender *et al.*, 2016; Griffen *et al.*, 2016; Jackson *et al.*, 2016).

The premise of my argument is that null models can only advance comprehension when deviations from their predictions advance mechanistic insight. That is, deviations from their predictions should point towards implications other than "the null model is incorrect". An example of a null model advancing comprehension, taken from biodiversity science, is the null model of biodiversity effects on ecosystem function (Baert *et al.*, 2017; Fox, 2005; Loreau & Hector, 2001). This null model is based on a clear and explicit assumption: interactions within species (i.e. among conspecifics) are equal to interactions among species (i.e. among heterospecifics). Given this assumption, it is mathematically inevitable that ecosystem functions stay constant with the number of species in the community. Exactly because of the clarity of the underlying assumption, deviations from the null model's predictions are

101 informative: they point towards interactions within and between species that are of unequal
102 strength.
103
104 Null models in multiple stressor and environmental change research make clear predictions
105 (e.g. effects add up when the model is additive). However, at the community- and ecosystem-
106 level, it is not clear on which hypothesis these predictions are based (Schäfer & Piggott, 2018).
107 Rather, the hypothesis seems to equal the prediction, which hampers inference and thus
108 scientific progress. Indeed, deviations from null model predictions only imply that the joint
109 effect is, for example, not additive. In what follows, I illustrate this point using classic theory
110 in community ecology and the case of species richness as an example of a community-level
111 variable. I do so by showing that there is no link between the sign and size of the deviations
112 from a null model and the community-level mechanisms causing these deviations. More
113 specifically, I show that the same mechanism can lead to different deviations (antagonism and
114 synergism), but also that the opposite holds true: two inherently different mechanisms can both
115 lead to the same deviation (e.g. antagonism).
116
117 I consider two species X and Y competing for two essential nutrients R_1 and R_2, according to
118 resource uptake theory (Chase & Leibold, 2003; Tilman, 1982), assuming Monod uptake and
119 optimal foraging (Tilman, 1982). In this model formulation, a species' competitive ability for
120 R_j is greater when its so-called R_j^* is lower:
121 $$R_j^* = (mK_j)/(r - m) \quad \text{(eq.1)}$$
122 where m, K_j, r represent a species' mortality rate, half-saturation constant for uptake of R_j, and
123 its maximum reproduction rate, respectively. The outcome of competition between X and Y
124 can be graphically determined by plotting the isoclines of both species in the resource place
125 (solid lines in Fig. 1). An isocline is a line that connects the combinations of R_1 and R_2 at which

126 a species is at equilibrium, and its location is fully defined by the species' R_1^* and R_2^*. Thus, the
127 two isoclines need to intersect for both species to have equilibrium densities at the same
128 combination of resource levels. In the example of Fig. 1, there is a trade-off in the ability to
129 take up nutrients: X is the best competitor for R_2 (R_2^* of X < R_2^* of Y) while Y is the best
130 competitor for R_1 (R_1^* of Y < R_1^* of X). This trade-off allows the intersection of the two
131 isoclines. However, this trade-off is a necessary but insufficient condition for coexistence: in
132 addition, the resource supply point must lie within the coexistence region (in grey in Fig. 1),
133 which is the region between the consumption vectors of both species (dashed lines in Fig. 1).
134 Given the assumption of optimal foraging, the consumption vectors are proportional to R^*; the
135 per-capita consumption rate of a species on resource i is $\frac{R_i^*}{y_i}$, with y_i the amount of biomass
136 produced per unit of resource i.



137

138 Figure 1: A plane of resource levels, containing two isoclines: one for species X (black), and
139 one for species Y (red). Parameters (m, K_1, K_2, r) are (0.3, 2.8, 1, 1) for species X, and (0.3, 1,
140 3, 1) for species Y. Therefore, R_1^* for X, $R_{1,X}^*$=1.20, $R_{2,X}^*$ =0.43, $R_{1,Y}^*$ =0.43, and $R_{2,Y}^*$ =1.29.
141 The dashed lines are the two species' consumption vectors according to optimal foraging. The
142 yield y is the same for both species (0.1). When the supply rate of both resources (dot) falls
143 within the zone (in grey) delimited by the consumption vectors, coexistence is possible.

I consider a first pair of environmental change drivers that both slow down resource uptake: they both increase the half-saturation constant K_2 of species X for R_2, and therefore R_2^* of X (eq.1), by a certain arbitrarily chosen factor (Fig. 2A-C). They do not affect any other parameters. A variety of mechanisms may underpin such effects. For example, temperature may alter nutrient-uptake proteins in plants (Giri *et al.*, 2017) and light-harvesting pigments in phytoplankton (Chalifour *et al.*, 2014), while ocean acidification can impair ciliary activity in mussels, decreasing feeding (Clements & Darrow, 2018). When present alone (Fig. 2A-B), both drivers do not affect species richness: the new coexistence region still comprises the resource supply point and so both species continue to coexist. However, when both drivers are present (Fig. 2C), the joint effect on species X's competitive ability is too large to maintain coexistence: the coexistence region does no longer contain the resource supply point. Hence, one species will go extinct. Thus, overall, the joint effect of these two drivers on species richness would be categorized as synergistic: the joint effect (a reduction from two to one species) is greater than expected from the single drivers, which have no effect on species richness when applied individually.

I now consider a second pair of drivers that work via the same mechanism as the first pair: both drivers again slow down resource uptake (Fig. 2D-F). However, in contrast to the first pair of drivers, both drivers now each target one specific species. This could be due to, for example, both species having different physiologies or resource uptake strategies, giving them different sensitivities to different stressors (Clements & Darrow, 2018; McMahon *et al.*, 2012; Mensens *et al.*, 2017). The first driver increases K_2 of species X (Fig. 2D), while the second driver increases K_1 of species Y (Fig. 2E). Again, they do not affect any other parameters. In both cases, the isoclines do not intersect anymore, so one species is excluded. However, when both drivers are present (Fig. 2F), the isoclines do intersect: the two drivers install a new trade-off

between the competitive abilities of species X and Y that saves them from extinction. Thus, the joint effect is smaller than expected based on the individual drivers. In a null model framework, this joint effect would be termed 'antagonistic'. Taken together, the two pairs of drivers (Fig. 2A-C and Fig. 2D-F) illustrate that the same mechanism (a reduction of resource uptake) can lead to both synergistic and antagonistic effects.

I now turn to a third pair of drivers (Fig. 2G-I) that act on different mechanisms than the two first pairs given above. One driver (Fig. 2G) does slow down resource uptake (now it increases K_2 of species Y) and leaves other parameters unchanged, as in the examples given before. However, the other driver corresponds to a decrease in the availability of R_1 (Fig. 2H). The first driver causes extinction of one species by shifting the coexistence region sufficiently up such that it no longer includes the supply point (Fig. 2G). The second driver causes extinction too, by moving the resource supply point outside of the coexistence region (Fig. 2H). When combined, the joint effect of both drivers on richness is zero: both species are able to coexist because the new resource supply point falls into the new coexistence region (Fig. 2I). Thus, the null model approach would classify the joint effect as antagonistic. Taken together, the second and third pair of drivers illustrate that two different mechanisms (Fig. 2F: reductions of resource uptake vs. Fig. 2I: a reduction of resource uptake combined with a resource shift) can both lead to the same deviation from a null model prediction, in this case an antagonistic effect.

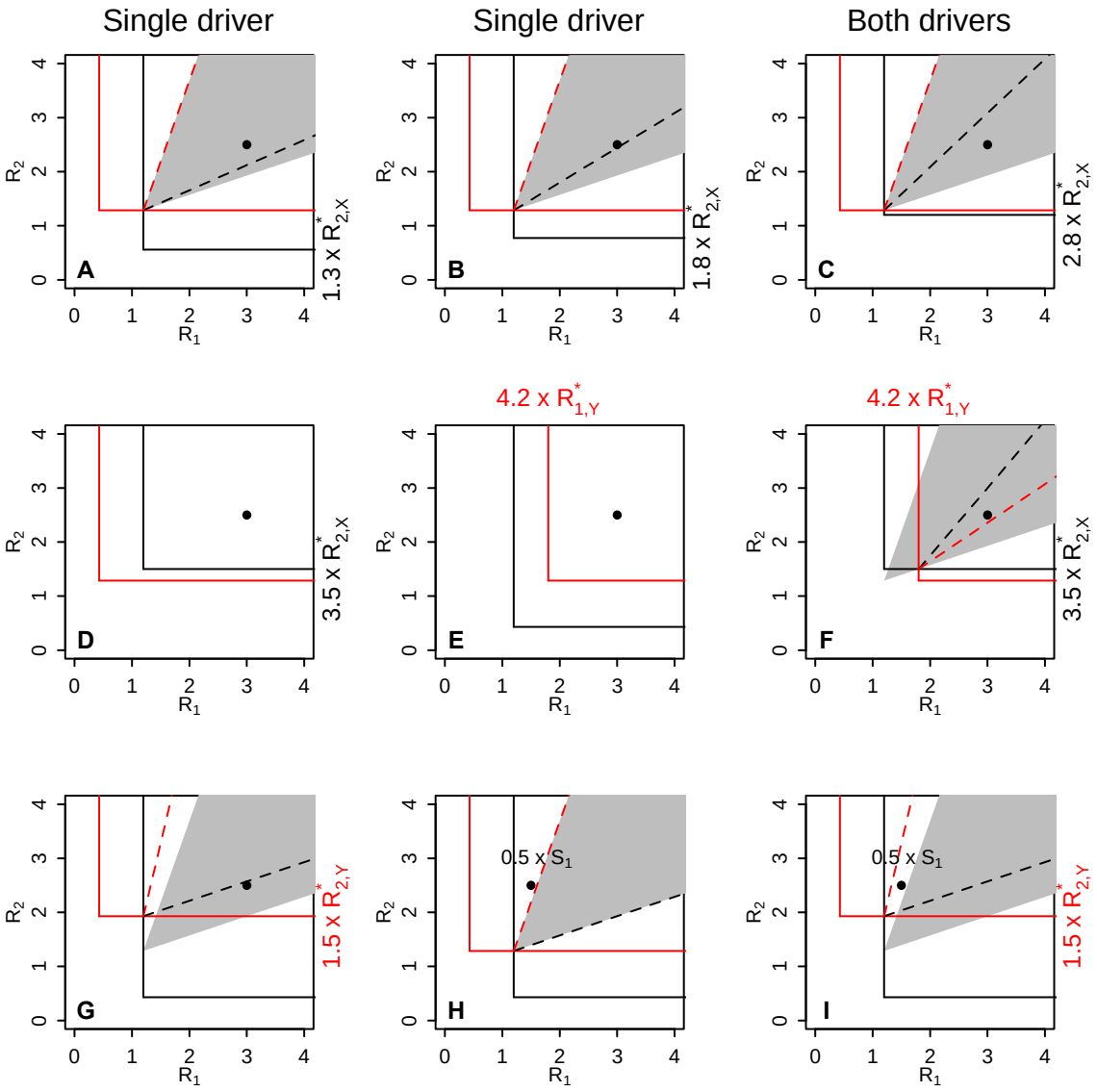


Figure 2: As Fig. 1, but now after exposure to one (panels A, B, D, E, G, H) or two environmental change drivers (columns C, F, I). Every row represents a different pair of drivers. The coexistence region in absence of change (in grey) is redrawn from Fig. 1 for comparison, unless when environmental change disrupts the intersection of isoclines and so removes the coexistence region (D, E). The numbers in black and red indicate the R^*values of species X and Y after modification by a stressor, respectively. The numbers inside panels H and I show the magnitude of resource supply shift.

One could argue that this example only shows that null models do not provide mechanistic insight, while they can still provide practical guidelines on how to manage ecosystems. Null models would allow grouping certain driver combinations that act, for example, synergistically. This information could be used for prioritisation and environmental decision making. However, the model illustration (Fig. 2) also shows that the deviations from null models will critically depend on the level of environmental change. For example, a smaller reduction of the resource uptake in Fig. 2G-I, or a larger reduction of R_1, would have resulted in different outcomes of how the joint effect is categorized. This illustrates the idea that information obtained from null models cannot be extrapolated beyond the tested ranges of the environmental change drivers (Schäfer & Piggott, 2018). This feature limits the capacity of null models to assist ecosystem management.

A new framework for community- and ecosystem-level effects of environmental changes

As illustrated above, the current null model approach does not enhance understanding of community- and ecosystem-level effects of multiple drivers. We therefore need to move away from null model testing and start constructing a mechanistic framework (Griffen *et al.*, 2016; Kroeker *et al.*, 2017), as has been recently initiated at the level of populations (Galic *et al.*, 2017; Hodgson *et al.*, 2017) and communities (Thompson *et al.*, 2018). Here, I propose such a framework and show that deviations from its predictions can be informative, exactly because the assumptions underlying the predictions are well-defined.

As a starting point, I propose to formalise "environmental change". I postulate that two main types of environmental change are resource supply shifts (Vitousek *et al.*, 1997) and the appearance of multiple abiotic stressors (Steinberg, 2012). The effects of resource supply shifts are a main ingredient of theoretical ecology, and so their effects on community and ecosystem

variables are well understood. Resource uptake theory (Armstrong & McGehee, 1976; Chase & Leibold, 2003; Harpole *et al.*, 2016; Hillebrand *et al.*, 2014; Huisman & Weissing, 1994; Tilman, 1982) predicts that an imbalance in resource supply, for example caused by changing nutrient loads, leads to biodiversity loss and altered ecosystem function (Loreau, 1998; Loreau, 2010) (e.g. as in Fig. 2H). Whether or not resource ratio shifts result in extinctions depends on the resource uptake traits of the species. Here, I define resource uptake traits (hereafter 'traits') as done by Litchman and Klausmeier (2008), i.e. as parameters of a resource uptake model. This definition is broadly applicable across a wide range of community types, including plankton (e.g. Edwards *et al.*, 2013), terrestrial plants (e.g. HilleRisLambers *et al.*, 2012) and animal consumers (Murdoch *et al.*, 2003), because resource uptake models are mathematically similar across community types. These traits mostly include half-saturation constants, conversion efficiencies from resource to biomass, and loss rates (Armstrong & McGehee, 1976; Harpole *et al.*, 2016; Hillebrand *et al.*, 2014; Huisman & Weissing, 1994; Tilman, 1982). These traits determine the location of the isoclines in Fig. 1 (e.g. half-saturation constants for nitrogen determine the R_N^*), and therefore predict the outcome of competition at a given resource supply ratio. These traits thus determine how a species will respond to its biotic and abiotic environment and determine its contribution to ecosystem function, which makes them both response and effect traits (Violle *et al.*, 2007).

Inspired by the early work of Tilman *et al.* (1981), I postulate that integrating multiple stressors into resource uptake theory makes for a comprehensive framework to study community- and ecosystem-level effects of multiple drivers, including stressors and resource shifts. Specifically, I propose to realise this integration by making traits multivariate functions of multiple stressors (Fig. 3). If we know the effects of multiple stressors on such traits we can make educated guesses of how these effects translate to changes of variables at the level of

communities (e.g. biodiversity) and ecosystems (e.g. function). Note that the framework allows stressors to affect multiple traits, contrary to the examples provided in Fig. 2. In addition, we can readily include the additional influence of resource ratio shifts, since these are by definition covered by resource uptake theory. In this paper, I illustrate the framework for the case of competitive communities. However, resource uptake theory is general, and can be extended to food-webs (Chesson & Kuang, 2008; Murdoch *et al.*, 2003). Importantly, it can also be used to study community assembly (Koffel *et al.*, 2018; Seabloom *et al.*, 2003) and meta-community dynamics (Haegeman & Loreau, 2015; Tilman, 1994), allowing the inclusion of invasive species and habitat fragmentation as environmental change drivers not included in the present paper.

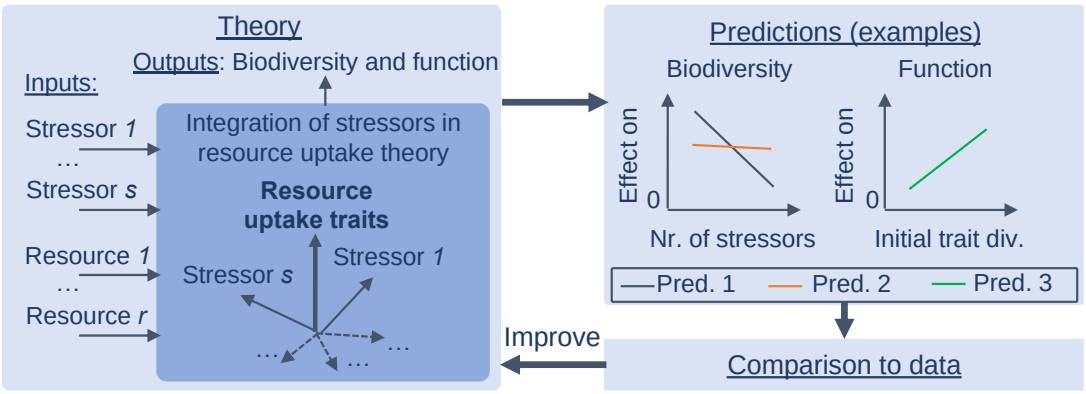


Figure 3: A proposed framework to study effects of multiple environmental changes on communities and ecosystems. Integrating multiple stressors into resource uptake theory yields predictions (pred.) regarding, for example, the influence of the number of stressors and the initial trait diversity of the exposed community on biodiversity and ecosystem function. Predictions 1-3 are detailed in the text. Comparing these predictions to experimental data can expose invalid assumptions underlying the theory, and therefore advances science.

How the new framework advances comprehension

The proposed framework advances comprehension in three ways: (1) by formalising exposure to multiple stressors using a set of key factors; (2) by producing a multitude of testable predictions on how these factors, alone and in combination with resource ratio shifts, affect communities and ecosystems; and (3) by quantifying and interpreting deviations between these predictions and observed effects.

I identify five factors that can describe the exposure to a given stressor combination in a formal way. This formalisation facilitates mechanistic progress because these factors are key determinants of community- and ecosystem-level variables such as biodiversity and function. A first and second factor are evidently the number of stressors and stressor response intensity. In line with Steudel *et al.* (2012), I define stressor response intensity (SRI) as the community average (i.e. across all species) of the absolute effect of a particular stressor combination on population growth (e.g. biomass or number of individuals) in monoculture:

$$SRI = E[|M - M'|/M]$$

where E, M, M' represent the expected value operator, monoculture growth in absence of the stressor cocktail and in presence of that cocktail, respectively. Note that SRI could also be defined at the level of the traits, representing the community-average effect on traits, and could include information on the sign of the effect in monoculture (i.e. growth stimulation or depression). SRI depends on the tolerance of the exposed species and the value of the stressors and is therefore often referred to as 'effect' (e.g. Liess *et al.*, 2016; Schäfer & Piggott, 2018). SRI and the number of stressors are typically not considered separately in experimental studies (Brennan & Collins, 2015). However, scientific progress demands understanding the contribution of both factors to the net effect. For example, in Fig. 2C, the factor causing extinction is SRI, rather than the number of stressors. Indeed, exposing the community to only

296 one of the stressors, but at a higher SRI, could have sufficed to cause an extinction. A third
297 factor is selectivity: the degree to which stressors affect all species or only a subset (De Laender
298 *et al.*, 2016). For selective stressors, also co-tolerance plays a role: species can be (in)tolerant
299 to multiple stressors at a time or not (Vinebrooke *et al.*, 2004). For example, in Fig. 2A-C, there
300 is positive co-tolerance, while in Fig. 2D-F, there is negative co-tolerance, with radically
301 different effects on species richness. This formalises the idea that selectivity is important only
302 when it implies greater stress to species with particular traits (Diaz *et al.*, 2013; Newbold *et al.*,
303 2015; Suding *et al.*, 2008). Selective stressors can therefore cause different effects on
304 biodiversity and function than unselective stressors (Mensens *et al.*, 2017; Selmants *et al.*,
305 2012; Spaak *et al.*, 2017). A fourth factor is initial trait diversity among species, which is
306 expected to determine resistance to stressors. Initial trait diversity implying larger niche
307 differences and smaller fitness differences will be better buffered (i.e. more resistant) to
308 stressor effects (Chesson, 2000). A fifth factor is the dynamic behaviour of stressors. Indeed,
309 stressors often fluctuate through time (Gunderson *et al.*, 2016), which can cause different
310 effects on coexistence (Chesson, 1994), and thus on biodiversity and function, than when
311 stressors remain constant through time.
312
313 Defining the five factors allows representing stressor combinations in a standardized way.
314 However, more importantly, we can make general predictions on how these factors matter for
315 the resulting community- and ecosystem-level effects (Fig. 3), and on how these factors
316 combine with resource ratio shifts. These predictions can offer scientists, working on a variety
317 of communities, theory-based and testable predictions that extend beyond the question if
318 effects are, for example, additive. More specifically, for various combinations of the number
319 of stressors, SRI, selectivity and co-tolerance, initial trait diversity, and temporal stressor
320 dynamics (constant, or various kinds of fluctuations, as in Jiang & Morin, 2004; Jiang & Morin,

2007), various aspects of biodiversity but also two types of ecosystem function (biomass production and resource uptake) can be predicted. Here, as an example, I provide five such predictions, of which three are illustrated in Fig. 3. The exhaustive analysis of how the five factors mentioned above together affect biodiversity and function is not an objective of the present opinion paper. Future theoretical contributions can address this question in full-factorial setups. Rather, I want to illustrate the kind of predictions the framework could produce. Afterwards, I discuss how these could be experimentally tested.

Prediction 1 postulates that, for selective stressors exhibiting negative co-tolerance (each stressor only affects one species), the effect on species richness decreases with the number of stressors. This is because, with an increasing number of stressors, but a constant SRI, an increasing number of species will be affected but to a smaller extent. When SRI is low, this will not affect the trade-offs that maintain composition and sustain function. When SRI is high, this can lead to new trade-offs being installed (e.g. Fig. 2F). Note that, for both low and high SRI, effects on biomass production can occur, leading to stressor effects on function in absence of effects on richness (Spaak *et al.*, 2017). Prediction 2 postulates that lower stressor selectivity results in smaller effects of the number of stressors on biodiversity and function. For example, when stressors are completely unselective, every stressor should affect every species to exactly the same extent. The number of stressors causing this effect is irrelevant. In the opposite case, when stressors are very selective, i.e. every stressor affects a different species, the number of affected species equals the number of stressors. A higher number of stressors thus means that more species are affected, but to a lesser extent (again, since SRI needs to stay constant). Prediction 3 postulates that the effects of selective stressors on function increase with initial trait diversity. For example, when initial trait diversity is small (all species have very similar trait values), small levels of selective stress can suffice to disrupt coexistence, leading to

diversity loss. However, since tolerant and sensitive species have very similar trait values, tolerant species will rapidly compensate for the lost biomass of the sensitive species and changes of function will be minor. When initial trait diversity is high, selective stress will be less likely to cause exclusion but effects on function can be more substantial because of a loss of functional complementarity. Prediction 4 postulates that fluctuations of stressors matter less when the number of stressors is low. This is because, when resource supply does not fluctuate, affecting few types (a consequence of the current example of high stressor selectivity) is less likely to cause large changes in resource levels. This reduces the covariation between environmental and competition effects on species' growth. Coexistence theory learns that this makes fluctuation-dependent coexistence mechanisms less important (Chesson, 1994). Finally, Fig. 2I illustrates prediction 5: stressors that reduce resource uptake can make community composition less resistant to resource ratio shifts. Indeed, the two stressors reduced the coexistence area, meaning that smaller shifts of resource ratio are needed to disrupt coexistence and cause extinction.

I propose testing predictions like those listed above using two approaches. A first approach could focus on 'high-level' predictions that transcend the specificities of model systems. Such high-level predictions exist in other research fields. Examples include the increase of ecosystem function with the number of functionally different species (Cardinale *et al.*, 2011), the effects of niche dimensionality on species diversity (Harpole *et al.*, 2016), and the effect of dispersal on regional biodiversity (Mouquet & Loreau, 2003). The proposed framework could be exploited to identify predictions about the effects of the number of stressors, *SRI*, and selectivity that are robust to other parameter settings. Monoculture experiments would then suffice to quantify *SRI* and selectivity for a given community composition exposed to a given stressor combination: resource uptake traits need not be measured. Thus, by selecting the right

371 combination of species and stressors, one can experimentally test high-level predictions on
372 how these factors, alone and combined with resource ratio shifts, affect biodiversity and
373 function.
374
375 A second approach is far more labour intensive and requires growing species in monoculture,
376 at various resource supply and stressor levels, to infer their traits and how these change with
377 stress. These data can then predict the outcome of competition at various combinations of
378 stressors and resource ratio shifts. Comparing these predictions to the actual outcome of
379 competition experiments is the strongest possible test of the theory. This approach is
380 conceptually similar to the work by Tilman *et al.* (1981) for the case of a single stressor,
381 temperature. However, the amount of work needed to apply this approach to multiple stressors
382 restricts this approach to microbial systems tested using high-throughput protocols (Altermatt
383 *et al.*, 2015), and makes it inapplicable to species with longer life cycles. Still, this approach
384 can lead to considerable progress in two ways. First, it would yield insight into which facets of
385 global change most disturb trade-offs that sustain biodiversity and functions in microbial
386 systems (Litchman *et al.*, 2015). Second, it would add environmental stress as a new dimension
387 to the classic topic of resource enrichment and niche dimensionality (Borer *et al.*, 2014;
388 Cardinale *et al.*, 2009; Harpole *et al.*, 2016; Hillebrand *et al.*, 2014).
389
390 One useful ingredient of the existing null model approach is the fact that it makes clear
391 predictions. Assessing the capacity and limitations of predictive capacity is indeed a central
392 goal in ecology and environmental science (Houlahan *et al.*, 2017; Petchey *et al.*, 2015).
393 However, the new framework I propose here allows studying not only predictive capacity but
394 also what drives predictive capacity, again because the assumptions are clear and are different
395 from the predictions. Thus, observations deviating from theoretical predictions (e.g.

predictions 1-5 listed above) point at invalid assumptions and thus expose areas of theory improvement, advancing science. For example, the theoretical approach I propose assumes that the interaction type does not change with SRI: resource competition is always the only interaction type. The only way stressors can change community dynamics is by changing resource uptake traits, and thus potentially competitive outcome. Regardless of the SRI, species always interact indirectly by relying on the same resources; they never interact directly. Thus, when species interaction types change profoundly with SRI we can expect theoretical predictions to become increasingly erroneous (Barton & Ives, 2014; Mulder *et al.*, 2001; Suttle *et al.*, 2007). More specifically, the stress gradient hypothesis postulates that competitive (i.e. negative) interactions would switch to facilitative (i.e. positive) interactions (Olsen *et al.*, 2016) as environmental change intensifies (i.e. the environment gets 'harsher', or SRI increases) (He & Bertness, 2014; Hines *et al.*, 2015; Maestre *et al.*, 2009; Mulder *et al.*, 2001). Thus, in community types where predictive capacity drops with SRI, more detailed studies could be set up to examine interaction types along stressor gradients. In an experimental study, Vanelslander *et al.* (2009) found that the marine diatom *Cylindrotheca closterium* grew better in medium containing substances leaked by other diatom species than in fresh medium. In a modelling study, Baert *et al.* (2016) inferred from experimental data that such facilitative interactions could be the exception rather than the rule in a similar community type evaluated along a pesticide gradient.

Another example of how the proposed theory could deviate from observed joint effects is through the influence of time. Again, the theory is very clear on how time is considered: it assumes traits to change instantly with the stressor level (Fig. 3). Community dynamics are therefore purely driven by external fluctuations in SRI, by the rate at which ecological interactions propagate these fluctuations to population growth, and by consumer-resource

421 dynamics internal to the system (Chesson, 1994; Huisman & Weissing, 1999). Thus, one can
422 expect a reduced predictive capacity when long-term effects on traits occur, e.g. due to
423 evolution or slow transgenerational plasticity (Doebeli & Ispolatov, 2014; Litchman *et al.*,
424 2015). This is because, in this case, the resulting long-term effects on biodiversity and function
425 will be unpredictable from short-term responses of traits to environmental change (Feckler *et*
426 *al.*, 2018; Turcotte & Levine, 2017). Microbial systems are well-suited to study such effects in
427 realistic time frames, as one can study adaptation of single strains to new environmental
428 conditions or altered fluctuation regimes, due to novel mutations or horizontal gene transfer
429 (Brennan & Collins, 2015; Collins *et al.*, 2014; Litchman *et al.*, 2015). For phytoplankton, such
430 events have been found to be more prevalent when the number of environmental drivers is
431 greater (Brennan *et al.*, 2017). Thus, when the predictive capacity of the proposed theory (Fig.
432 3) decreases with the number of generations and does so more when the number of drivers is
433 higher, this could stimulate studies on, for example, the adaptation of resource uptake traits.
434
435 Both examples given here of how the proposed theory could misjudge the effects of the number
436 and kind of drivers on communities and ecosystems align with the idea that science benefits
437 from 'breaking models' when these models have formal assumptions (Thiele & Grimm, 2015).
438 Indeed, this practice not only identifies follow-up studies on facilitation and trait adaptation
439 but will also lead to extensions of the theory. Resource uptake theory can be extended with
440 equations for exudate production and uptake (Van den Meersche *et al.*, 2004), and for long-
441 term trait change. As a starting point for long-term trait change, one could consider approaches
442 from quantitative genetics, allowing to make various assumptions on the direction and rate of
443 trait adaptation along gradients of environmental change (Barabás & D'Andrea, 2016; Chevin
444 *et al.*, 2010; Schreiber *et al.*, 2011).
445

Conclusions

In order to advance understanding of how multiple drivers of environmental change affect communities and ecosystems, we need to move away from testing null models: they lack a mechanistic basis and deviations from, or correspondence to, observations can therefore not advance insight. Here, I propose to base predictions on ecological theory and interpret deviations from observations as an essential step to meet the scientific and societal challenge of understanding global change effects. The approach I advocate here can probably be generalized to other organizational levels, because quantitative frameworks are available to predict physiological effects of multiple stressors at the individual and population level, including bio-energetic models (Sokolova, 2013) and dynamic energy budget models coupled with individual-based models (Galic *et al.*, 2017; Goussen *et al.*, 2016).

At present, there is a tendency to label deviations from additivity as 'ecological surprises' (Brook *et al.*, 2008; Crain *et al.*, 2008; Darling & Cote, 2008; Thompson *et al.*, 2018), implying they are not to be expected ('surprising') on the basis of ecological science. However, synergistic and antagonistic effects can be expected from basic ecological science and are therefore no ecological surprises (Fig. 2 and Halstead *et al.*, 2014). The proposed framework provides better guidance as to which driver combinations provoke truly surprising effects, i.e. effects that are not expected from one of ecology's most established theories but triggered by emergent processes such as stress-induced facilitation and trait adaptation.

Figure captions

Embedded in the text.

Figures

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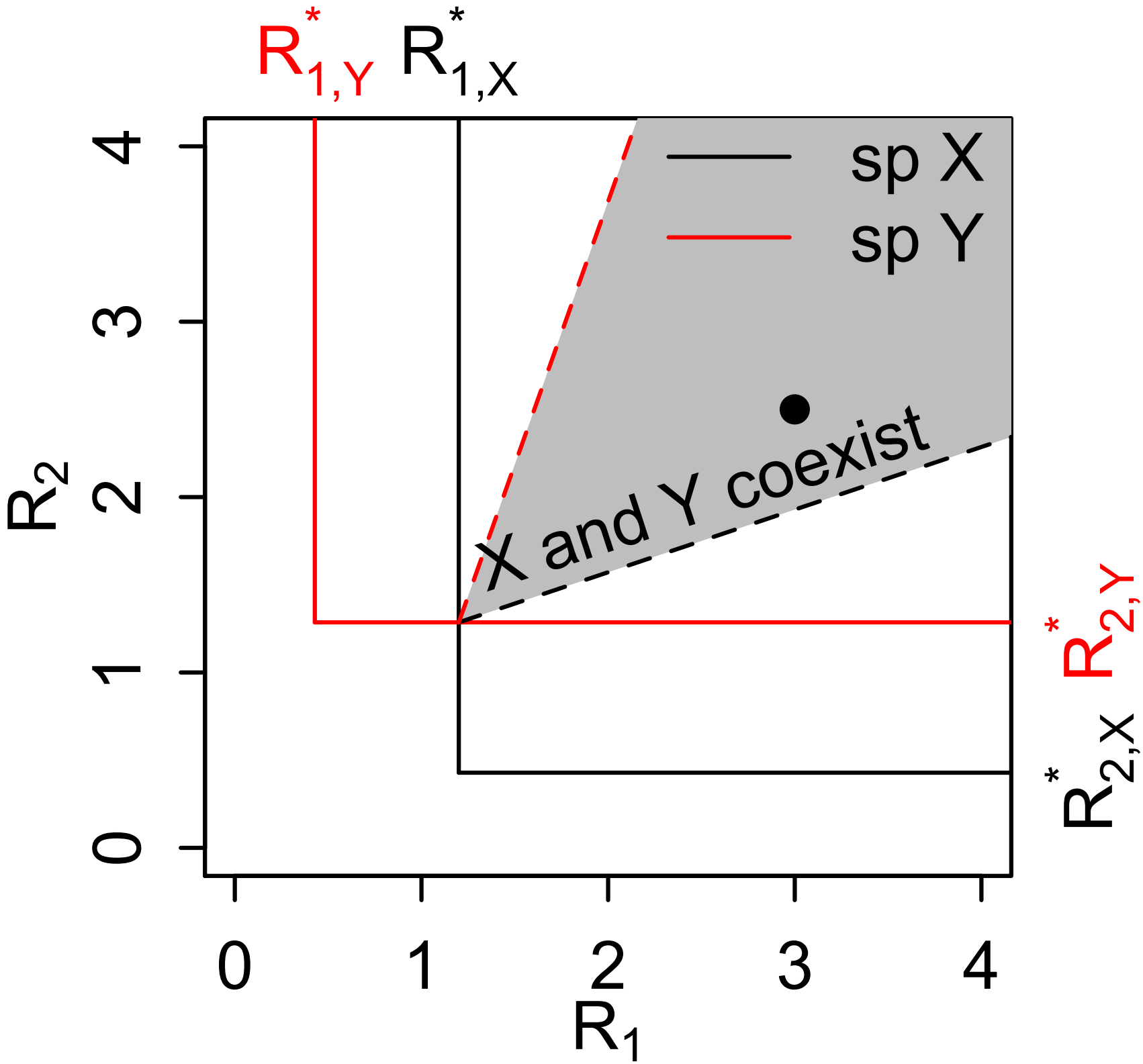
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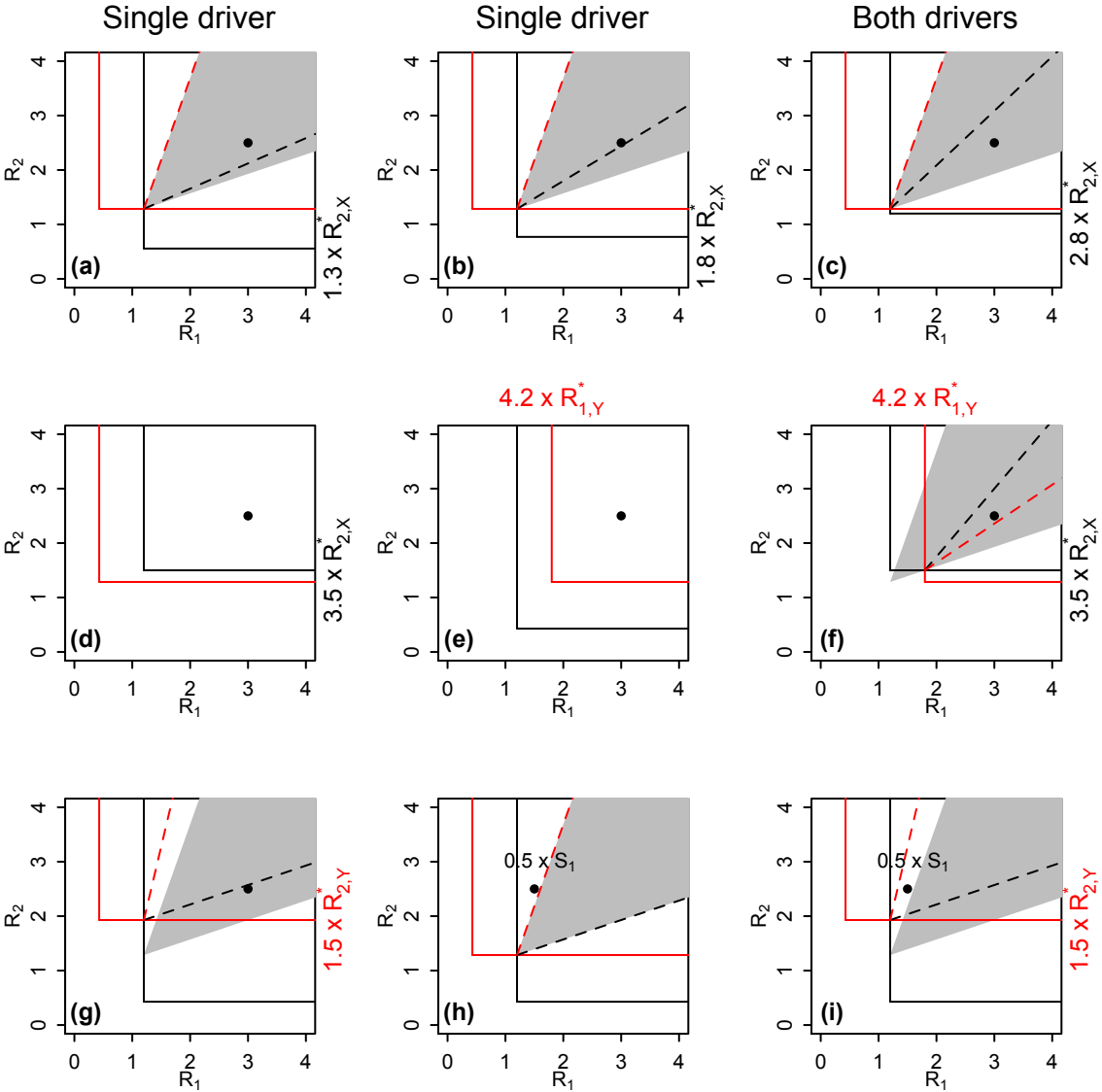
Single driver
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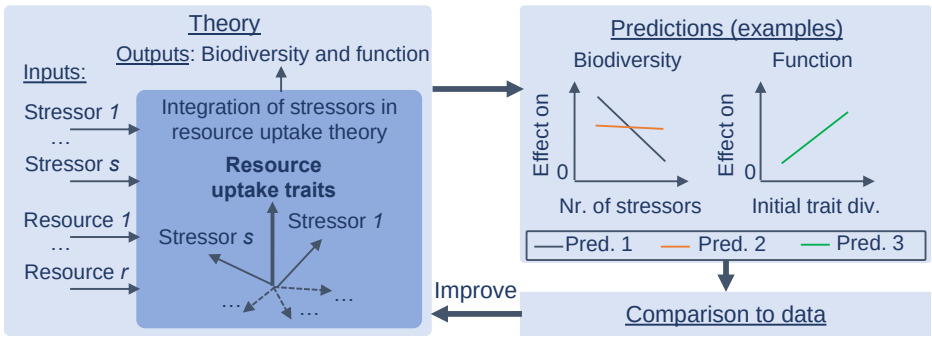
1.5 x R*2,Y
0.5 x S1


Theory
Outputs: Biodiversity and function
Inputs:
Stressor 1
…
Stressor s
Resource 1
…
Resource r
Integration of stressors in resource uptake theory
Resource uptake traits
Stressor s
Stressor 1
Predictions (examples)
Biodiversity
Function
Effect on
0
Nr. of stressors
Effect on
0
Initial trait div.
Pred. 1
Pred. 2
Pred. 3
Improve
Comparison to data